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Microbial Communities

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Invisible to the scrutiny of naturalists, most microbial communities have escaped description

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Microbes, often studied as disease "germs," are not generally considered in context as normal components of ecosystems. For one thing, their ubiquity and density tend to be underestimated. Although the notion of species as borrowed from the animal world is probably invalid for microbes (Sonea and Panisset 1983), we are talking about over 200,000 different types of organisms. These include about 20,000 prokaryotes (Starr et al. 1983), over 100,000 protoctists (Corliss 1984, Margulis et al. 1986a), and some 100,000 fungi (Ainsworth and Sussman 1978). The vast majority of these microbes do not cause diseases in humans or other mammals. Neither are they all decomposers. Every sort of nutritional mode exists among microbes: photoautotrophy, chemoautotrophy, heterotrophy (including osmotrophy, symbiotrophy, necrotrophy, and phagotrophy). Some bacteria *(Bdellovibrio, Vampirococcus, Daptobacter)* even prey actively on other bacteria (Guerrero et al. 1986). Although some microbes are cosmopolitan and others are extremely restricted in distribution, they may be as well integrated into community structure as any plant or animal.

Sections through a termite intestine, a mudflat, and colored lake water reveal well-structured communities

Yet because they are invisible to the scrutiny of naturalists, most microbial communities have escaped description. Community ecologists, who have the background to analyze microbial communities, usually lack formal training in the microbial and microscopic methods needed to distinguish the member populations. Moreover, the first step in traditional microbial studies requires removing the organisms from their communities (Sonea and Panisset 1983). But recent work by a growing number of scientists who begin to call themselves microbial ecologists (and to publish in journals like *Microbial Ecology* and *Applied and Environmental Microbiology*) is starting to change this picture.

Microbial communities, which offer enormous potential for study, have lately been recognized as sources of crucial information about the biosphere (Cohen et al. 1984, Lapo 1982), including the atmosphere (Lovelock 1979) and ancient sediments (Krumbein 1983, Margulis et al. 1983). At least some microbial communities are tightly organized and demonstrate phenomena well known in ecology, such as dominant species and succession (Atlas and Bartha 1981, Stolz 1984b). Indeed, microbial communities can provide us with unique live systems that can be used to test general concepts about how natural populations are organized. They occupy little volume and grow rapidly and are thus far more manageable than, for example, forest or desert communities. Furthermore, the complexity of every community is augmented by its underlying, surrounding, and penetrating microbial communities. For these reasons, microbial communities lacking plants and animals are in principle less complex and more amenable to study than communities of larger organisms.

Taxonomically, microbial communities comprise primarily members of two kingdoms: Monerans (prokaryotes: all bacteria including cyanobacteria) and Protoctista (eukaryotic microbes: protists and their multicellular descendants excluded from the plant, animal, or fungal kingdoms; Margulis and Schwartz 1982). Occasionally, fungi and microscopic animals such as rotifers and nematodes may also be regular members of microbial communities. But in contrast to well-known macroscopic communities of animals and plants, most

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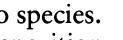
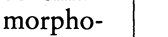
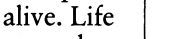
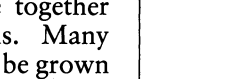
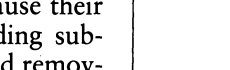
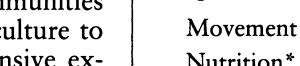
members of well-studied microbial communities have not been identified even to genus; very few microbes in nature have been identified to species.

Microbial community composition remains difficult to pinpoint, in part, because the organisms are so small that most cannot be studied morphologically while they are still alive. Life cycles are difficult to piece together from electron micrographs. Many bacteria and protists cannot be grown in isolation (axenically) because their growth requirements, including subtleties like gas production and removal, are not known. Typical microbiological identification techniques (see box, right) have limited use. Removing microbes from their communities and growing them in pure culture to identify them requires expensive experimentation by highly trained people. Many microbes form specific associations and attachments with others and thus cannot be cultivated alone. The metabolic or structural bases for these difficulties are seldom understood, but many researchers have observed that morphologically complex and metabolically interesting microbes (often dominant members of their communities, e.g., *Mixotricha, Arthromitus,* and *Staurojoenina*) resist attempts to grow them in pure culture (Cohen et al. 1984).

Although not all significant details are available, enough is known to permit us to describe here three very different microbial communities: a cellulolytic community from the intestines of dry wood–eating termites (To et al. 1980), a marine subtropical intertidal benthic community (microbial mats) (Cohen et al. 1984), and a photosynthetic community from a freshwater, sulfur-rich upland lake (Guerrero et al. 1985).

Several principles emerge from our examples. Under highly specific climatic and physical conditions, recognizable microbial communities begin to form, grow, and develop in a rapid but standard successional manner (Goldsmith 1985). The boundaries, or ecotones, of these communities are as distinguishable as those of their larger counterparts. In our examples, species that are members of these communities are unique to them. We found not a single example where a recognizable bacterium or protist species belonged to more than one com-

Microbiological identification criteria

Criterion	Value
Morphology and grouping of cells	Rod 
	Coccus 
	Vibrio 
	Spirillum 
	Spirochete 
	Filamentous Simple or branching  Coryneform 
	Fruiting structure 
Gram stain	Positive or negative (correlated with presence of outer lipid membrane in the Gram negative cell wall) 
Spores	Form or do not form 
Movement	Nonmotile, flagellated, gliding 
Nutrition*	Heterotroph
	Autotroph: photo- or chemo- (Source of carbon—organic or inorganic as CO_2—and source of energy—chemical inorganic, organic, or light—is determined. Metabolic details are then worked out, e.g., metabolic products and ability to break down polysaccharides.)
Response to oxygen*	Obligate anaerobe
	Aerotolerant anaerobe
	Facultative anaerobe
	Obligate aerobe: Microaerophil (less than 20% O_2 optimum) Aerophil (20% or greater optimum)
Response to other environmental variables*	
Temperature	Steno- or eurythermic
Salt	Steno- or euryhalic
	Halophilic, marine, freshwater (optimum growth at salinities above seawater; optimum growth at or below seawater salinities, sodium requiring; optimal growth in fresh water)
Pressure	Steno- or eurybaric
Acidity	Steno- or eury-acid-tolerant
Examples of other traits	Colony morphology, size on defined media
	Production of acid or gas during growth
	Percent G+C: $\frac{G+C}{(A+T)+(G+C)} \times 100$ in DNA†
	Pigment production: chlorophylls, carotenoids, prodigiosin, etc.
	Enzyme tests: catalase, oxidase, lysine, decarboxylase reactions, etc.
	Specific metabolic abilities: sulfate reduction to sulfide, nitrate reduction to gaseous nitrogen and nitrous oxide, nitrogen fixation, methanogenesis, sulfur and sulfide oxidation to sulfate, ammonia oxidation to nitrate and nitrous oxides as sources of energy, etc.
	Antibiotic sensitivities

*Testing for these criteria requires growing axenic microbial cultures.
†G, guanine; C, cytosine; A, adenine; T, thymine.

munity. We shall see that the curious naturalist is no more likely to find *Trichonympha* in a sulfurous Spanish lake or a laminated microbial mat than one is likely to find a flamingo in the Gobi Desert. Just as those studying Amazonian forests, sphagnum bogs, or southern English hedgerows have observed, knowledge of one or two indicator species in a community may help predict many of its other aspects.

Communities and ecosystems

Since a good deal of inconsistency and unstated assumptions exist in the use of words across various biological disciplines, we would like to be precise about the following terms: *association, symbiosis, population, community,* and *ecosystem.* Associations include relationships of all kinds among organisms of different species. From a nutritional viewpoint, associations may range from necrotrophic (one partner deriving food from a second such that the second partner is eventually debilitated and may die [pathogenic to parasitic]) to biotrophic (nutritional exchange between partners such that they both survive [parasitic to mutualistic]). Symbiosis refers to the physical proximity of individuals of different species throughout a significant portion of their life cycles. Depending on environmental factors that change through time, symbiotic associations may vary from casual (not required for either partner) to obligate (required for both partners).

Populations are individuals of the same species living together in the same place at the same time. Communities, groups of heterogeneous populations, comprise members of different species living together at the same place and the same time. Ecosystems, made up of member communities, are larger biological units. For a set of associations to be identified as an ecosystem, the biologically significant elements, such as organic or mineral nutrients (carbon, hydrogen, oxygen, phosphorus, nitrogen, sulfur, sodium, potassium, and so forth), must cycle entirely within the system. These critical elements must cycle more rapidly within the system than among systems. Thus, forests, grasslands, salt marshes, and tundra are ecosystems, where the different organisms found in a termite hindgut, a microbial mat, or a lake are only communities until demonstrated otherwise.

An ecosystem invariably has a productive component, either photosynthetic or chemoautotrophic. In light, bacteria, algae, or plants are the photosynthetic producers, whereas in energy-rich dark environments supplied with the appropriate chemicals, chemoautotrophic producers (e.g., sulfur-, iron-, ammonia-, or methane-oxidizing bacteria) are the producers. In addition, an ecosystem must have algivore, bacteriovore, or predator components; they must also harbor degradative species. These may include myxobacteria, labyrinthulids, ciliates, acrasiads, chytrids, carrion-eating birds, or scavenging mammals, but they always include osmotrophs (usually protoctists, fungi, and bacteria) that feed on the others, recycling the biochemicals in the bodies of the producers and consumers. Therefore, careful study could reveal that the microbial mat and upland lake communities we describe are indeed ecosystems (since both of them harbor autotrophs, consumers, and decomposers). However, the termite hindgut community, which lacks producers—it has neither photoautotrophic nor chemoautotrophic members—cannot be an ecosystem.

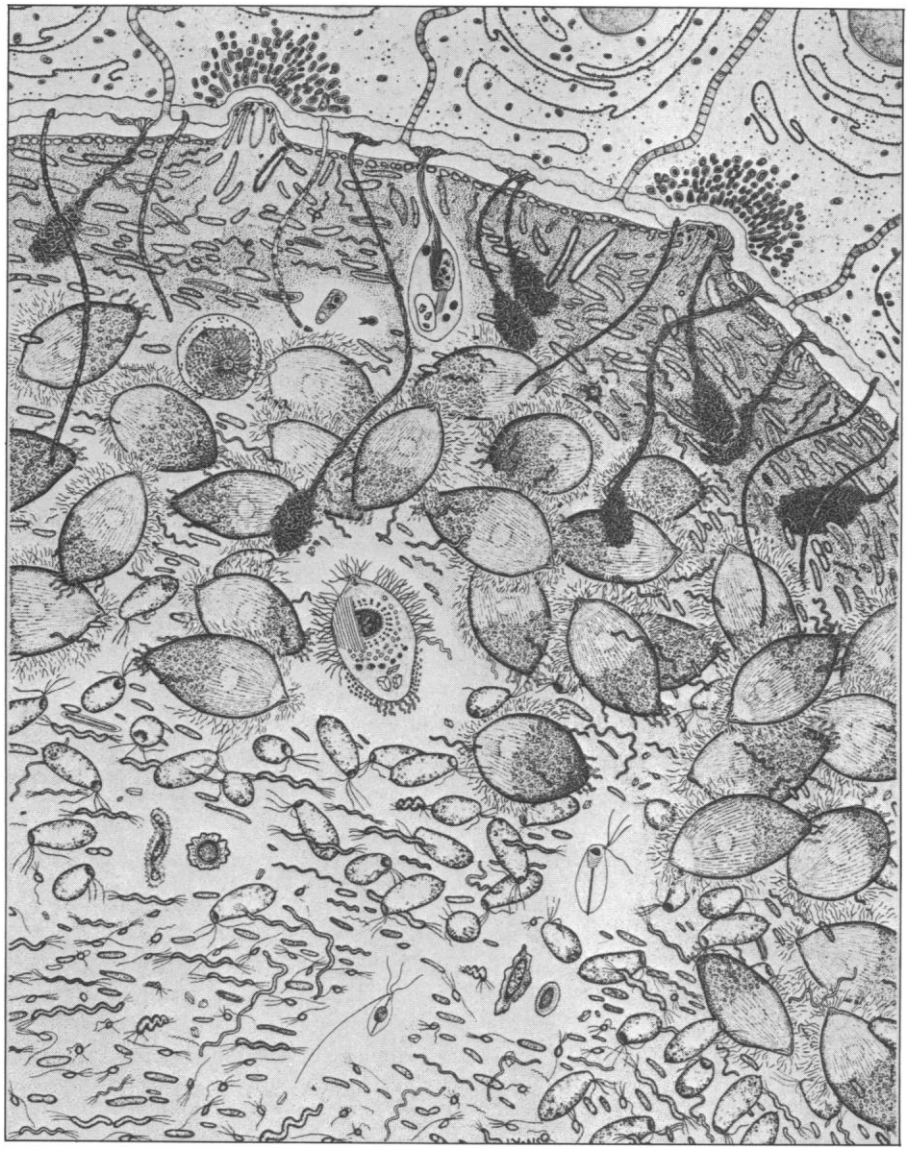


Figure 1. Microbial community of a termite hindgut. The cells at the top are the gut tissue cells of a *Pterotermes occidentis* pseudergate (worker). Drawing by Christie Lyons.

Microbial communities in termite intestines

There are over 350 species of dry wood–eating termites, or kalotermitids, primarily inhabitants of tropical and subtropical forests. There are also more than 150 subterranean species of termites called rhinotermitids. All those species investigated from both groups harbor in their hypertrophied intestine called the hindgut, or paunch, complex microbial communities like those shown in Figure 1 (Breznak 1982, Cleveland 1934, Yamin 1982).

Nutrition is the major explanation for the existence of insect hindgut microbes. Although larval and nymph termites have pincer mandibles adapted to ingesting wood, they lack cellulase enzymes and cannot, therefore, digest it. Wood-eating forms nevertheless derive their carbon entirely from the wood in which they both nest and feed. Their nitrogen may come from some six sources: (1) It can be recycled within a colony when termites ingest the corpses of conspecifics; (2) a tiny amount of nitrogen is recovered from the wood; (3) some nitrogen comes from digesting the hindgut microbes themselves, (4) some from the fungi the termites ingest with the wood, and (5) termite uric acid—waste nitrogen—is recycled in usable form by the gut bacteria. Probably the most important net source of new nitrogen, however, is (6) from the anaerobic nitrogen-fixing bacteria that have been detected in the hindgut microbial community itself (Potrikus and Breznak 1981).

Microbial population densities, at least in the Sonoran desert termite *Pterotermes occidentis,* are 10^9–10^{11} prokaryotes and 10^4–10^6 eukaryotes per milliliter of hindgut fluid (To et al. 1980). The absolute numbers in these populations depend on the size of the microbe in question; smaller forms are more numerous. There are from about 4 to about 30 different species of protists in a wood-eating termite gut, depending on the termite species. Some mastigotes, such as *Staurojoenina* shown in Figure 2, are shockingly complex and covered with tightly associated bacteria. In addition to the motile cellulolytic protists, such as the many species of *Trichonympha* (Figure 3), there are probably dozens of bacterial species. Because of their morphological similarities and the difficulty in culturing most of them, an accurate estimate of termite bacterial diversity is not yet possible.

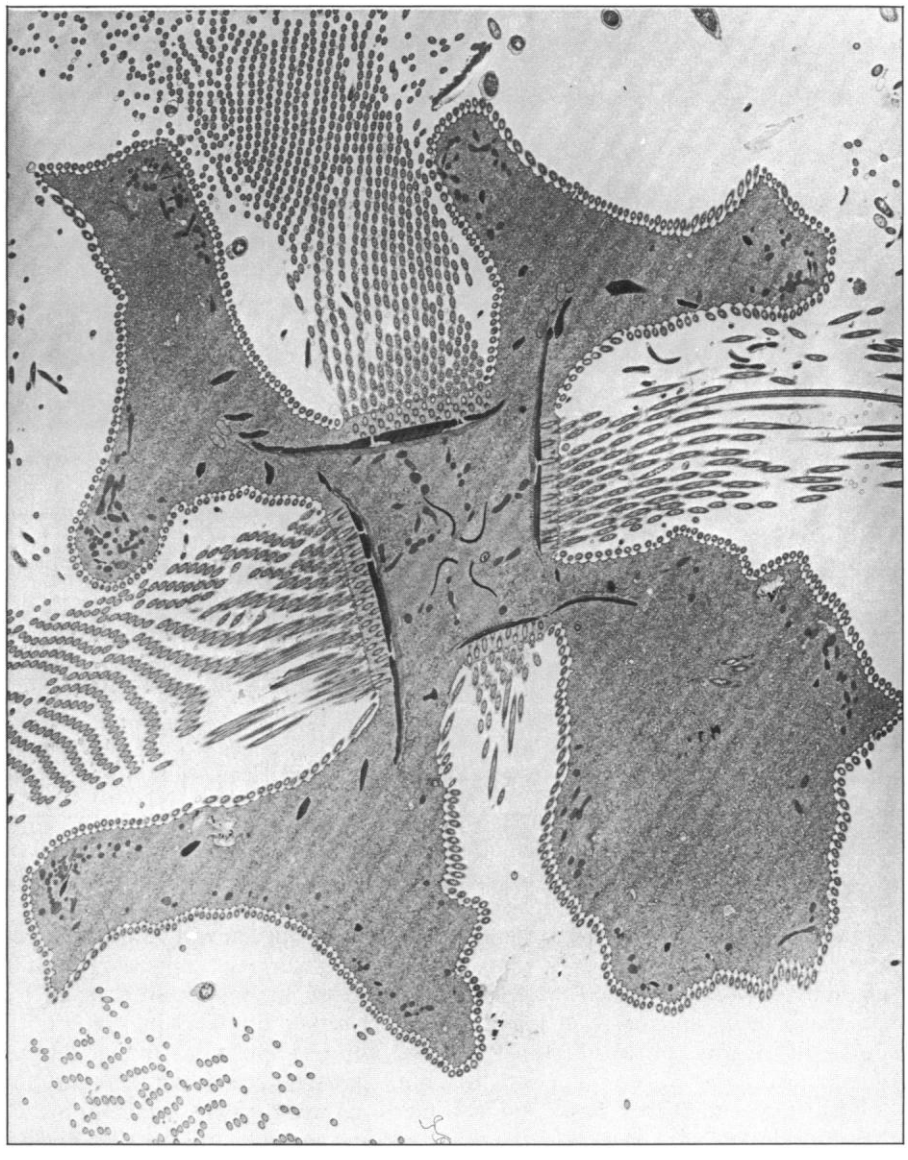


Figure 2. *Staurojoenina assimilis,* complex wood-ingesting mastigote from a termite; see also Figure 5. Transmission electron microscope (TEM) section through anterior portion of undulipodiated cell; × 3720.

Many kinds of protists and bacteria coexist in healthy termite hindguts. Only if the termites suffer starvation, heat, or other debilitating conditions does the community drastically change: A typical dry wood–eating termite with few or no microbes in its intestine is dying (Grosovsky and Margulis 1982). If the normal microbiota is not reintroduced, and the termite is not returned to the proper environment, it will die within a week or so.

Hindgut communities are described in this article for two termite genera, *Reticulitermes* and *Pterotermes*. *R. flavipes,* a well-known northeast American subterranean termite, ranges from Florida to Canada. *Reticulitermes hesperus,* another common subterranean termite, nests underground in California and other western states. Both species have specialized pockets in their gut linings, apparently to accommodate attached microbes (Figure 4a). *Pterotermes,* considered morphologically and behaviorally closer to ancestral wood-eating cockroaches, has similar gut-microbe associations but no pockets (Figure 4b). *Pterotermes* is far more

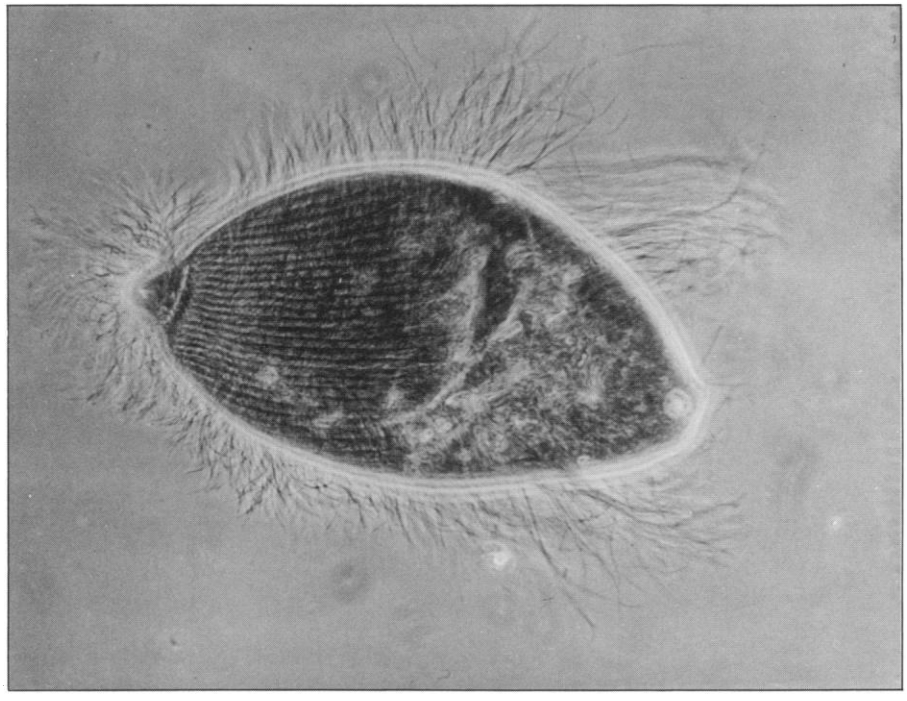


Figure 3. *Trichonympha ampla* from *Pterotermes occidentis* has wood particles in its posterior cytoplasm and spirochetes attached to its posterior end. × 318.

limited in distribution than *Reticulitermes:* it is entirely restricted to the Sonoran desert of eastern California, southern Arizona, and the state of Sonora, Mexico. The genus is represented by only one species, *P. occidentis,* which feeds and nests in logs of the leguminous palo verde tree *(Cercidium).*

Termite gut microbes have apparently developed various strategies to avoid being expelled by defecation or to survive being expelled: attachment or motility. The attached forms adhere either to the gut wall or to one another by specialized elaboration of their outer surfaces (Figure 5). In our studies, we have seen surface bacteria-bacteria, bacteria-protist (with and without specialization of one or both partners), and intracellular (including intranuclear) associations.

Many bacteria and protists are capable of swimming vigorously, presumably upstream in the gut. Some filamentous termite bacteria, such as several species of *Arthromitus* (Figure 6), distribute themselves to new gut attachment sites by forming spores able to grow some distance from the parent cells. These spores, released into the intestine, may land elsewhere in the gut lining and germinate. Already equipped with filaments, the spores are prepared to attach quickly to the gut.

The termites shed their microbial communities when they molt, discarding the entire hindgut as a package. Healthy microbes protected from the outside world are passed to newly hatched eggs and to newly molted individuals by proctodial feeding: an infected termite presents its hind end to the mouth of an uninfected individual. Once exposed to inhospitable conditions outside the intestine, the hindgut organisms die. Only in wood-eating cockroaches, presumed ancestors to termites, do members of the microbial community make hard-walled cysts, thus surviving desiccation and starvation in gut tissue packages until they are reintroduced into new insects. Because termite gut microbes cannot survive even ten minutes' direct exposure to air, their growth is apparently restricted to life inside the gut of active animals—and probably has been so restricted since the late Paleozoic when wood-eating cockroaches and termites first evolved (Cleveland 1934). The ubiquity of the diverse and peculiar hind-

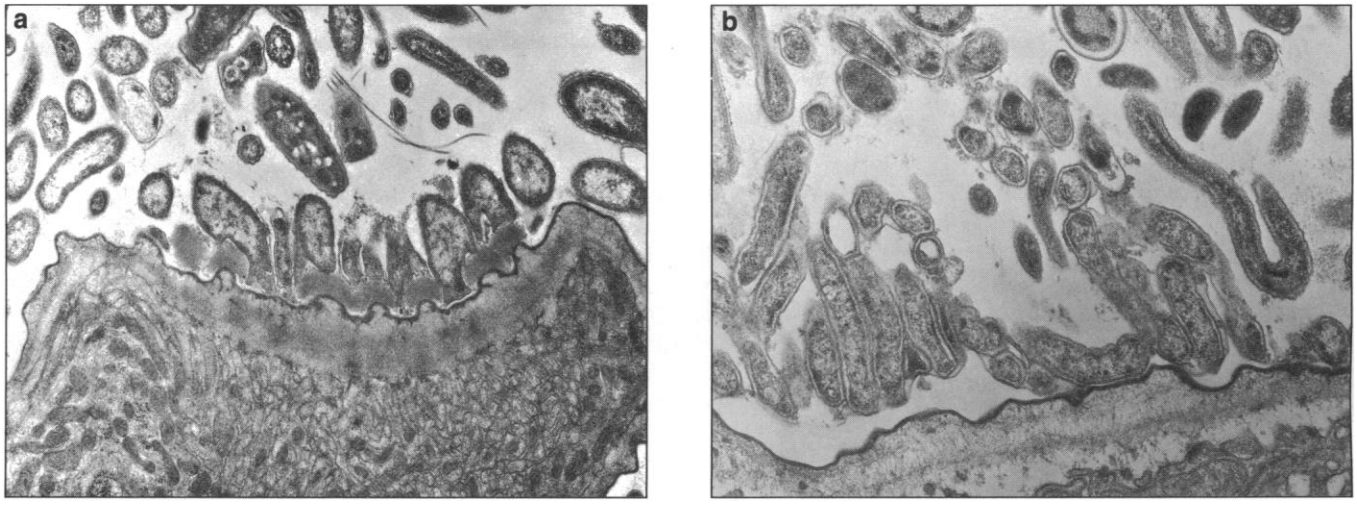


Figure 4a. Pocket in the gut lining of *Reticulitermes hesperus,* showing gut microbes attached to the chitinous insect tissue. **b.** Gut tissue of *Pterotermes occidentis* showing attached microbes and chitin layer. Electron micrographs, × 14,400 and 18,000.

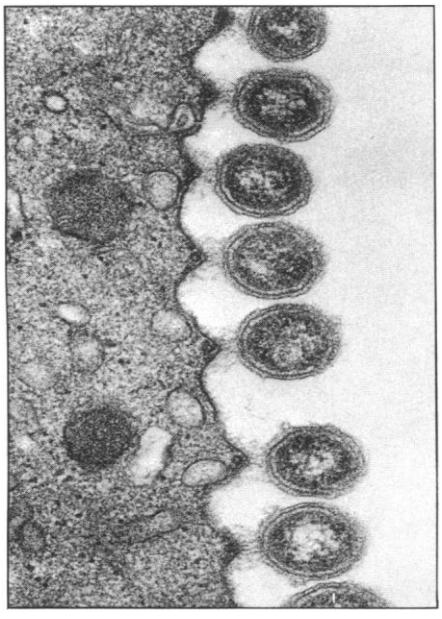


Figure 5. Evenly spaced surface bacteria, function unknown, with their attachment fibrils abutting raised portions of the surface of *Staurojoenina assimilis* (see Figure 2). The termite host is a dry wood–eating termite from California, *Incisitermes minor* (≡ *Kalotermes minor*). × 54,000.

gut microbiota in all these insects suggests that their common ancestors—probably mud and cellulose eaters—formed associations with microbes and have coevolved with them for over 200 million years.

Microbial mats in evaporite flats

An entirely different sort of microbial community grows in restricted sites along the western coast of Baja California Norte, Mexico. We have found stratified microbial communities in evaporite flats at only three locations in Laguna Figueroa, just north of San Quintín. These communities are dominated by a large filamentous cyanobacterium, *Microcoleus cthonoplastes*. The flat microbial mats form in tidal channels where seawater percolates daily beneath the sand dunes, providing an environment for the growth and accretion of laminated sediments under the influence of *Microcoleus* and other members of its highly structured community (Figure 7). The photosynthetic members of the community include well-known, fast-growing, nitrogen-fixing cyanobacteria such as the filamentous *Nostoc, Anabaena,* and *Nodularia,* as well as other common "weedy" cyanobacteria such as *Spirulina* and *Oscillatoria.*

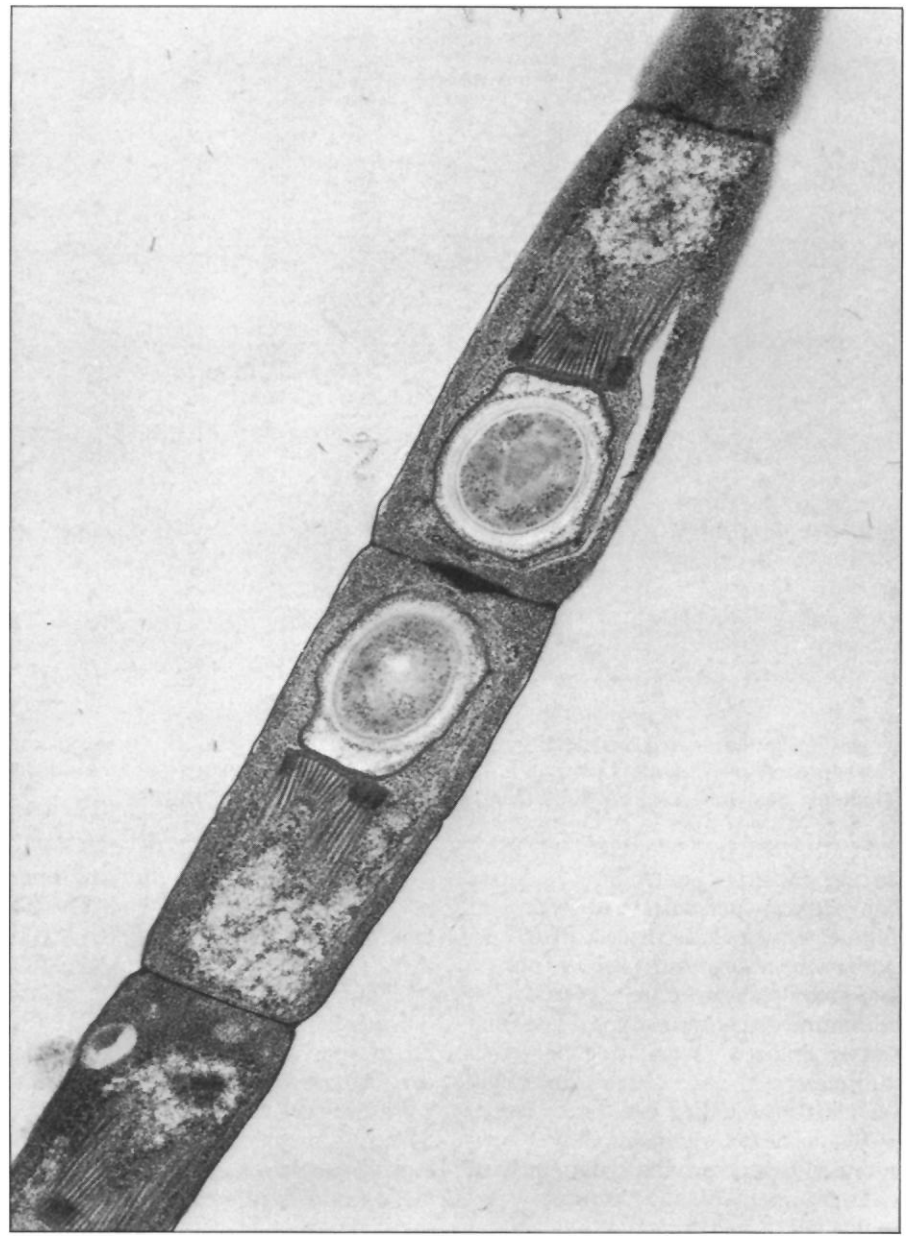


Figure 6. *Arthromitus* sp., anaerobic filamentous spore-forming bacterium from the hindgut community of *Reticulitermes tibialis*. Each cell forms endospores with conspicuous spore-attachment filaments. × 34,500.

Although many cyanobacteria can be isolated and grown from mat material, the cyanobacteria most responsible for the texture and growth pattern of living mats are *Microcoleus cthonoplastes* (see Figure 7). An unidentified coccoid-pleurocapsalean-like cyanobacterium and an unidentified filamentous cyanobacterium also add to the mats' cohesive, fibrous textures. None of these sheathed oxygen-producing photosynthetic bacteria have been grown axenically.

The morphological differentiation of the mat community is analogous to the epidermal and dermal tissue of mammalian skin. The topmost cyanobacteria lie just below the evaporite sediment layer. Below the cyanobacterial layer, anaerobic purple phototrophic organisms predominate. And below the purple layer lives a black layer dominated by various poorly known heterotrophic and sulfate-re-

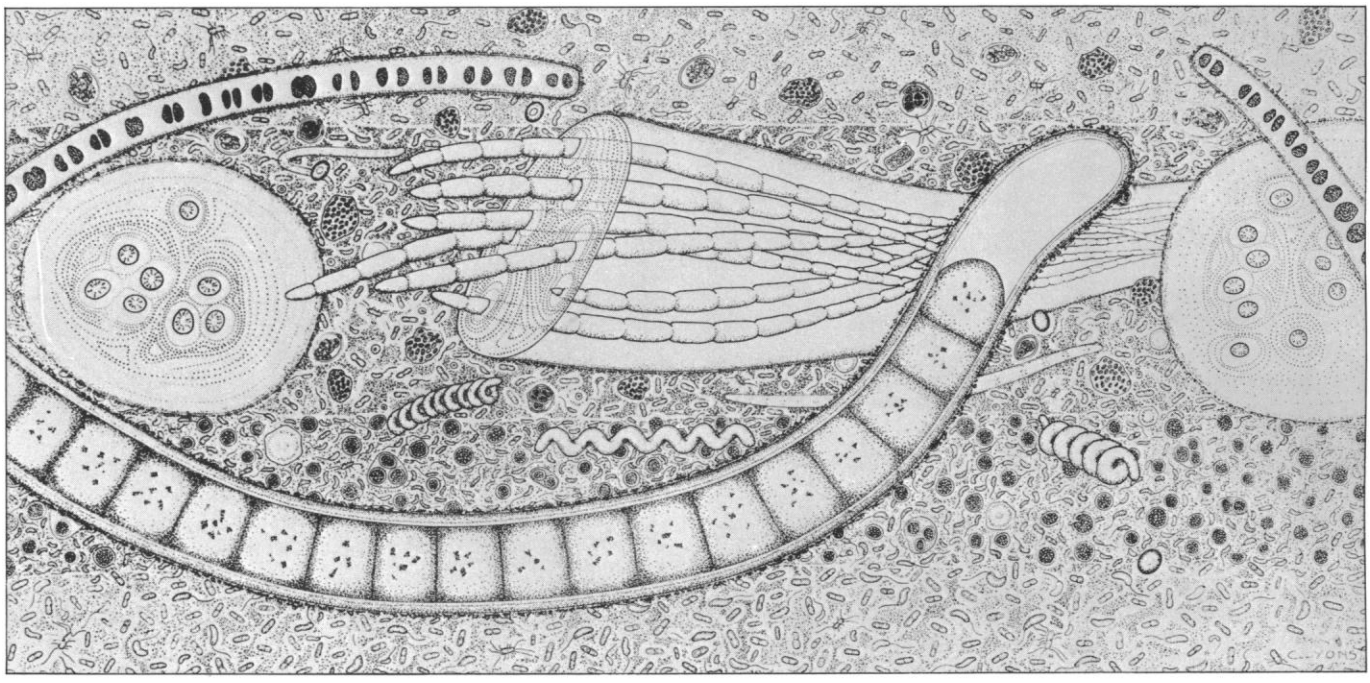


Figure 7. Flat laminated microbial mat dominated by *Microcoleus,* the organisms that look like thickly insulated telephone cables. This drawing by Christie Lyons is based on detailed ultrastructural observations of Stolz (1984b) and the discovery of a flat laminated mat in Matanzas, Cuba (Margulis et al. 1986b).

ducing bacteria (Figure 8). The latter convert seawater sulfate to hydrogen sulfide, which is used as a hydrogen donor in photosynthesis by purple and green phototrophic bacteria. This community structure appears as distinctly colored layers, one or fewer millimeters thick, which are easily seen with the naked eye.

Many new organisms have been revealed from studying sediment with electron-microscopic techniques originally developed for studying animal tissue (Stolz 1984a). Microbial mats are placed whole into fixative, embedded in plastic, and thin-sectioned as if they were liver or bone. The flat mats that form the laminated structures have been studied at the EM level since 1977 (Stolz 1983).

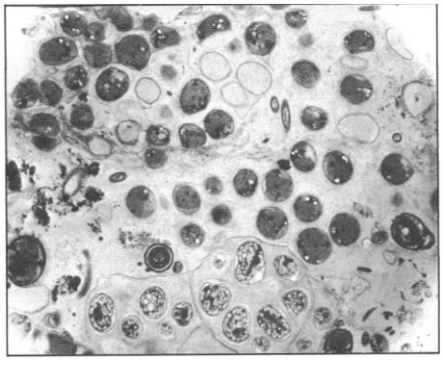


Figure 8. Purple photosynthetic bacteria from below *Microcoleus* layer in the flat mat. × 3675.

During fierce inundations in 1978–80 in southern and Baja California, the *Microcoleus*-dominated mats were entirely flooded and destroyed by standing fresh water. Classic ecological succession followed, in which it took approximately five years from the destruction of the climax community to its reappearance (Stolz 1984b, Stolz and Margulis 1984). The mat-building climax *Microcoleus* community was replaced by heterotrophs, purple sulfur phototrophic bacteria that have not yet been described in the scientific literature, a bloom of a new strain of an amoebomastigote, *Paratetramitus jugosus,* and other microbes. *Microcoleus* and the organisms generally accompanying it in the original mat community swam or glided away or drowned, disappearing entirely. But by the end of summer 1983, mat organisms from the channel edges were again recolonizing. Thus, microbial communities appear to display the same phenomena of ecological succession as do any biological communities, only faster.

Although the termite hindgut and the hypersaline microbial mat communities have not a single known member species in common, community layering can be seen in both. Whereas the lumen of the termite intestine leads to a radial layering, that in the mat community is flat. Microbes, like all organisms, are aligned in their surroundings in positions determined by the environment's chemical, physical, and biological properties. In bodies of water such as fjords and freshwater lakes, microbial stratification can be seen and studied far more easily than in the complex and tiny termite and mat communities (Nealson 1983). We turn next to such a community, one resembling the mats more than the termite gut community, but whose vertical stratification is stretched out over decimeters, even meters, instead of fewer than millimeters.

Microbial communities of anaerobic sulfurous lakes

Probably the world's best studied of these communities is the one in Lake Cisó, a small body of water 300 meters west of Lake Banyoles in Girona, northeast Spain (Guerrero et al.

1985). Hemispherical, only nine meters deep at its deepest, and covering just 487 m^2, Lake Cisó harbors a bacterial community that is far less complex but more accessible to study than those of either termite hindguts or microbial mats. This freshwater upland lake, 175 m above sea level, is unusual in that anoxygenic phototrophic bacteria can be found throughout the water column during the entire year. The major microbial populations can therefore be described and their changes monitored as a function of measurable environmental variables.

The surface of Lake Cisó shows remarkable color differences, from clear to bright red to brown, which reflect the photosynthetic pigments of the bacterial inhabitants. Except for ciliates and mastigotes that feed on bacteria and occasional blooms of green algae that develop when winds aerate the top few centimeters of the surface, the lake is devoid of eukaryotes. It is dominated by three major populations of anaerobic bacteria: two in the water column and one in the sediment. *Chromatium,* a reddish purple sulfur phototrophic bacterium, belongs to the same family as *Thiocapsa* from Laguna Figueroa but differs from the mat organisms in having motile, flagellated single cells and living planktonically. *Chlorobium,* a smaller, green phototrophic sulfur bacterium, also lives suspended in the water. In the sediment are various noncolored desulfovibrios (sulfate-reducing gram negative bacteria) that feed on organic matter and convert sulfate, found in solution, to hydrogen sulfide gas.

The lake's dramatic color changes are essentially due to periodic population shifts; the numbers of the phototrophic bacteria change. Remarkable color shifts such as these can be seen more in Lake Cisó than in other lakes, not because similar changes in bacteria populations do not occur elsewhere—they do—but because they occur very close to the surface and are therefore obvious. Why? The lake is fed by seepage from waters that pass through rich layers of gypsum ($CaSO_4 \cdot 2H_2O$) and thus supply relatively high quantities of sulfate to it. This sulfate is converted by desulfovibrios to hydrogen sulfide, which rises through the water. Since Lake Cisó is relatively shallow and protected by a thick barrier of trees and shrubs from winds that tend to oxygenate top waters, for many months in the year the sulfide can reach well-lit zones at the surface. The combination of oxygen-poor with light- and sulfide-rich conditions favors the growth of the two brightly colored organisms, *Chlorobium* and *Chromatium* (Figure 9).

Both of these phototrophic bacteria require H_2S for growth. Unlike oxygen-producing phototrophic organisms (cyanobacteria, algae, plants) that split H from H_2O, the anoxygenic phototrophic bacteria of Lake Cisó split H from H_2S, giving off sulfur as a waste product of H_2S-using photosynthesis. The elemental sulfur is deposited as globules inside *Chromatium* cells, but is extruded from *Chlorobium* cells into the water.

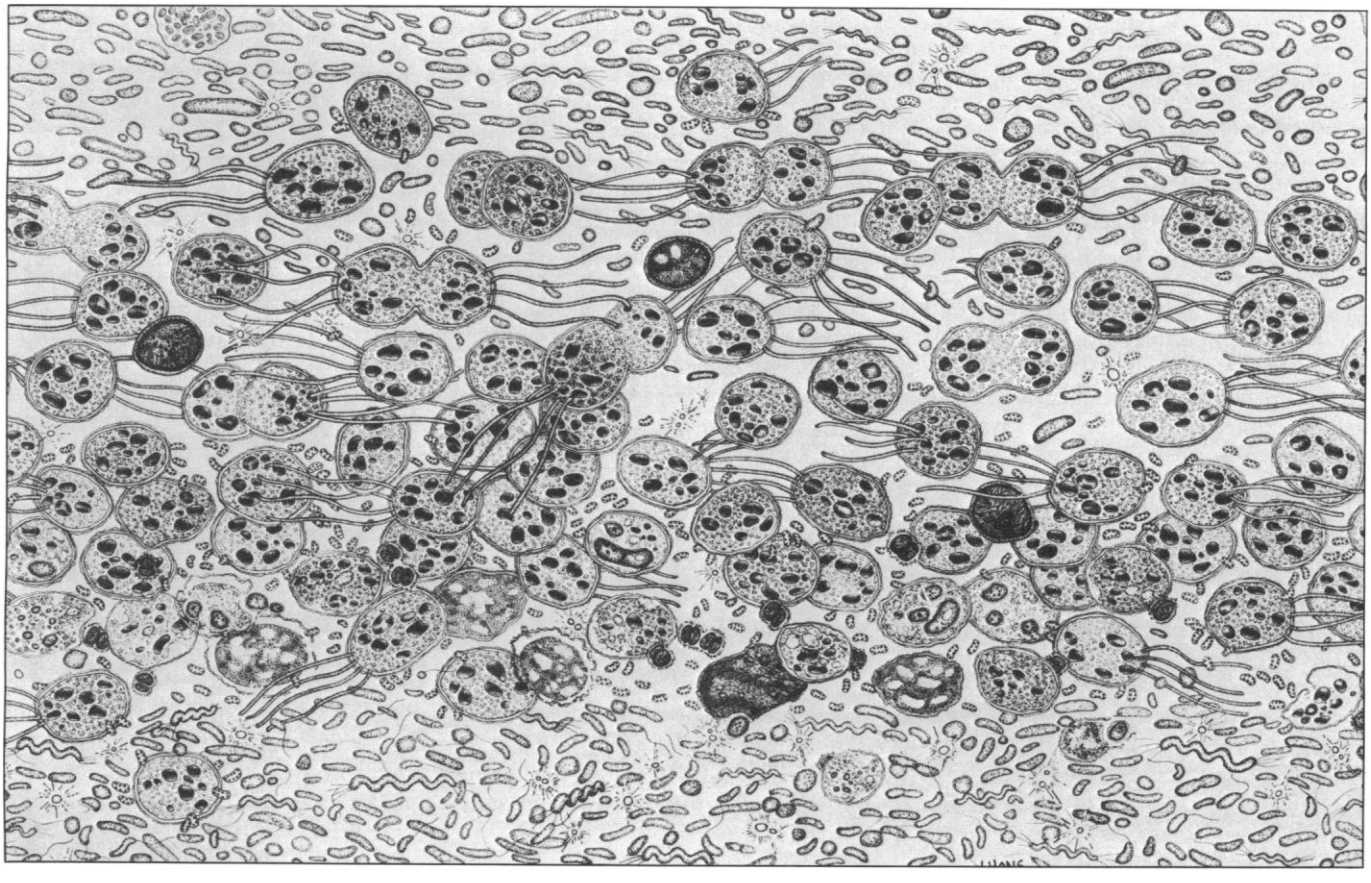


Figure 9. *Chromatium* community: microbial purple layer of Lake Cisó. About 10^7 cells are present per milliliter of lake water. Drawing by Christie Lyons.

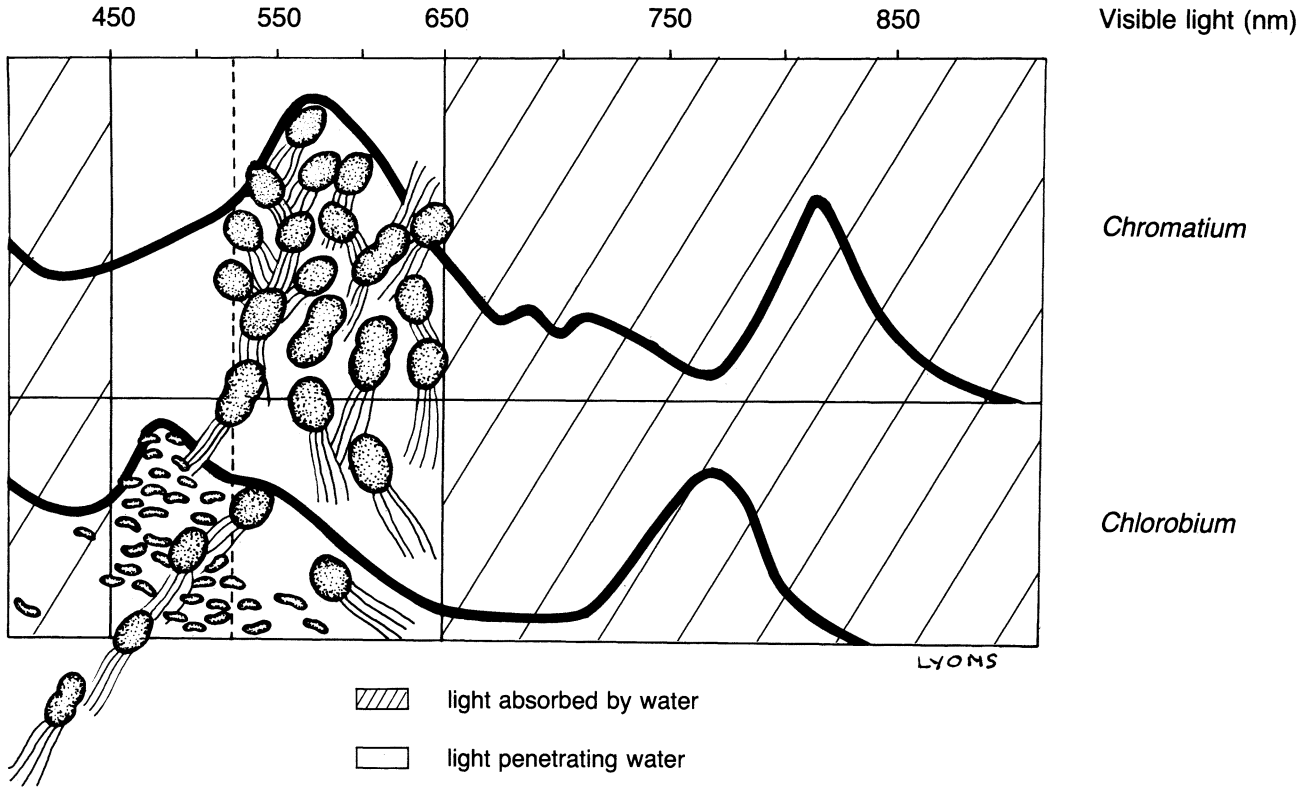


Figure 10. Light absorption (*y* axis) as a function of wavelength in *Chromatium* and *Chlorobium*. Each bacterial population migrates to its position of maximum light absorption. *Chromatium* cells contain pigments that absorb at longer wavelengths than those of *Chlorobium*, which can therefore take advantage of light between 450 and 500 nm. When *Chromatium* is absent, *Chlorobium* can also use light from 450 to over 550 nm. In nature, neither population can use wavelengths shorter than 450 nm or longer than 600 nm because these wavelengths have already been absorbed by the water itself (cross-hatched area). Drawing by Christie Lyons.

As these two bacterial populations become larger, they form colored layers in the water; *Chromatium* forms the top layer a meter or less above *Chlorobium*. The reason: *Chromatium* is flagellated, and because it is attracted continuously by the light, it swims toward the surface. *Chromatium* requires more light to grow than *Chlorobium* does; it is also more tolerant of oxygen and less tolerant of high hydrogen sulfide concentrations. The *Chlorobium* cells, which are unable to swim and are highly oxygen-sensitive, grow just beneath *Chromatium*—out of the way of stray oxygen and where there is plenty of H_2S for photosynthesis. Furthermore, *Chromatium* cells shade the light from other *Chromatium* cells just below. This lack of appropriate light tends to be disastrous for the lower levels of this bacterial layer, where cells begin to die and sink. *Chlorobium* cells, whose pigments differ from those of *Chromatium*, can, however, scavenge the light just below the red *Chromatium* level (Figure 10). The biomass of *Chlorobium* is inversely proportional to the pigment concentration of *Chromatium*. *Chlorobium* reaches greater biomass in the lake when *Chromatium* pigment does not block the light, either because there are fewer total *Chromatium* or there is less pigment per *Chromatium* cell.

For some two weeks, Lake Cisó supports actively growing blooms—a thin layer of red *Chromatium* (about 10 cm) underlain by a similarly thin green layer of *Chlorobium* in which population growth persists until light, oxygen, sulfide, temperature, or other critical environmental variables limit it. Invariably, the *Chromatium* bloom is followed by bust; in less than a week the bright red can disappear. At least in part, this disappearance is due to predation by two newly discovered bacteria, *Vampirococcus* and *Daptobacter* (Guerrero et al. 1986).

Although the cyclical disappearance of *Chromatium* after a bloom has not been entirely explained, there are plausible hypotheses, which may all be partially correct. *Chromatium* is light limited, it is sulfide poisoned, or it is attacked by the bacterial predators *Vampirococcus* and *Daptobacter* (Figure 11). Because *Chromatium* cells in bloom block their own light, nearly all actively dividing cells are found at the very top of the *Chromatium* layer, often only a few centimeters from the surface. The greatest biomass of *Chromatium* cells, however, is below this dividing layer, usually by a few centimeters. At greater depths, perhaps a few meters, alive but inactive *Chromatium* cells will be found sinking. These cells survive by using up reserves of sulfur globules and organic storage products that they accumulated when they were photosynthesizing and growing in the light. When reilluminated, these *Chromatium* cells resume active growth. The energy produced by mobilizing their storage products is not enough to power their flagella (a highly energy-consuming process),

and therefore they cannot swim up to the light. Below several meters, *Chromatium* can no longer recover even if replaced into the light. The bodies continue to sink to the sediment on the lake's sides and bottom, providing a carbon source for desulfovibrios in the bottom layer.

The rapid production of sulfide from sulfate by desulfovibrios depends heavily on the supply of organic matter—dead *Chromatium* bodies, for example. Hydrogen sulfide makes its way through the water column and begins poisoning everything sensitive to it, including, perhaps, the bottom of the actively growing *Chromatium* layer itself.

Large numbers of small bacteria attaching to the degrading *Chromatium* cells have been seen, always a little after the *Chromatium* population reaches its maximum in the water column (Guerrero et al. 1986). These epibiotic bacteria are predators on the debilitated *Chromatium*. Epibionts (*Vampirococcus*) only divide if they are attached to *Chromatium;* their growth seems to depend on resources they can "suck" out of *Chromatium* cells (see Figure 11). A second type of predatory bacteria, *Daptobacter,* also attacks various chromatia. Penetrating *Chromatium's* gram negative cell walls, daptobacters reproduce inside under either aerobic or anaerobic conditions (Guerrero et al. 1986). Neither of these predatory bacteria attack *Chlorobium,* which may account for the fact that after the *Chromatium* bloom is gone, *Chlorobium* persists in the better-lit, high-sulfide conditions prevailing in the lake.

Lake Cisó's microbial community can be thought of as analogous to a multicellular organism whose dimensions are determined by those of the lake basin. Inside these limits, cells interact both cooperatively and antagonistically. They lower the local hydrogen sulfide concentration for one another; they provide necessary organic compounds to one another; they shade one another, compete for resources, and excrete toxic wastes. Each of the stratified planktonic phototrophic communities reproduces only at a given position in its vertical distribution—at the top of the red and green layers, respectively. The only reproduction by cell division of

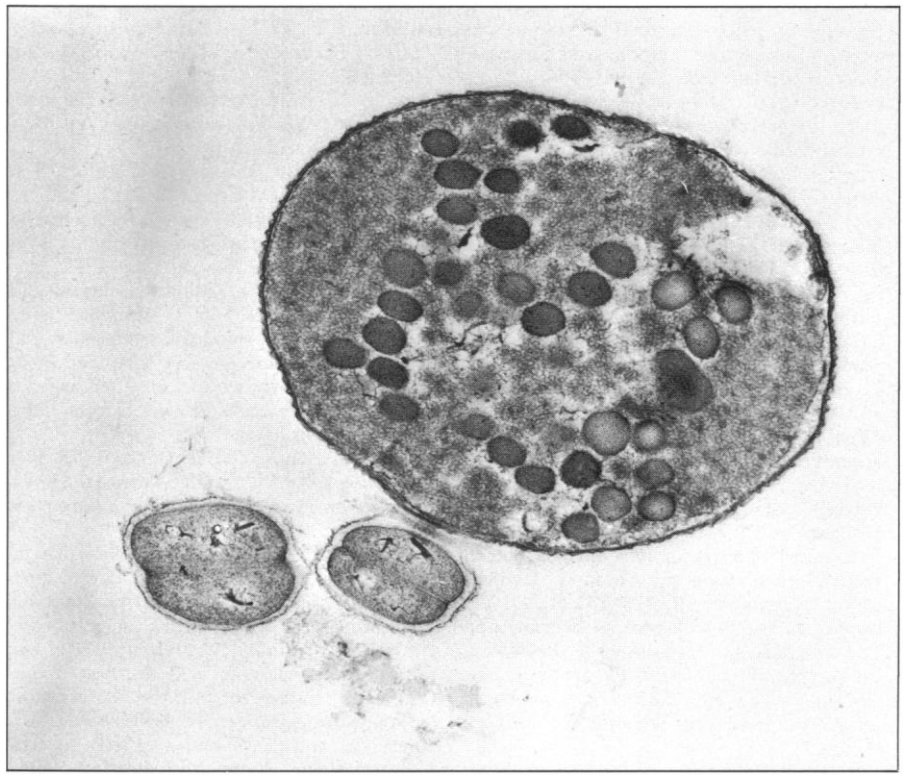


Figure 11. *Vampirococcus,* predator on *Chromatium minus,* kills it by "sucking out" its innards. *Vampirococcus* cells divide only if attached to *Chromatium.* × 21,280.

Chromatium and *Chlorobium* that occurs in the lake occurs in these layers; thus, we can compare these layers to reproductive tissue in multicellular organisms. The products of reproduction slowly sediment to the bottom; their bodies provide organic carbon for the sulfate-reducing bacteria, which then excrete the hydrogen sulfide to replenish the cycle. From a holistic perspective, as long as at least one or more cells of each microbial species survives and is capable of exponential growth, neither the continued survival of other individual cells or populations is necessary for maintaining the entire community through time.

A single population, like that of *Chromatium* in Lake Cisó, in the absence of its other community members will always grow, leading to its own destruction. This, of course, is a familiar fact to all microbiologists who maintain pure cultures of microbes. Diversity in nature is not a charming luxury but an absolute necessity for any ecosystem to function.

Thus we have seen that to form any natural community, qualitatively different populations must be present. The same energy sources and environmental restraints that have led to the grouping of animals and plants into functional aquatic, marine, and forest communities led much earlier to the evolution of complex microbial associations like those we describe here. Such dynamic, yet cyclically stable communities have not only persisted through geological time, but their continued existence is essential for the element cycling on which our much larger animal and plant communities depend.

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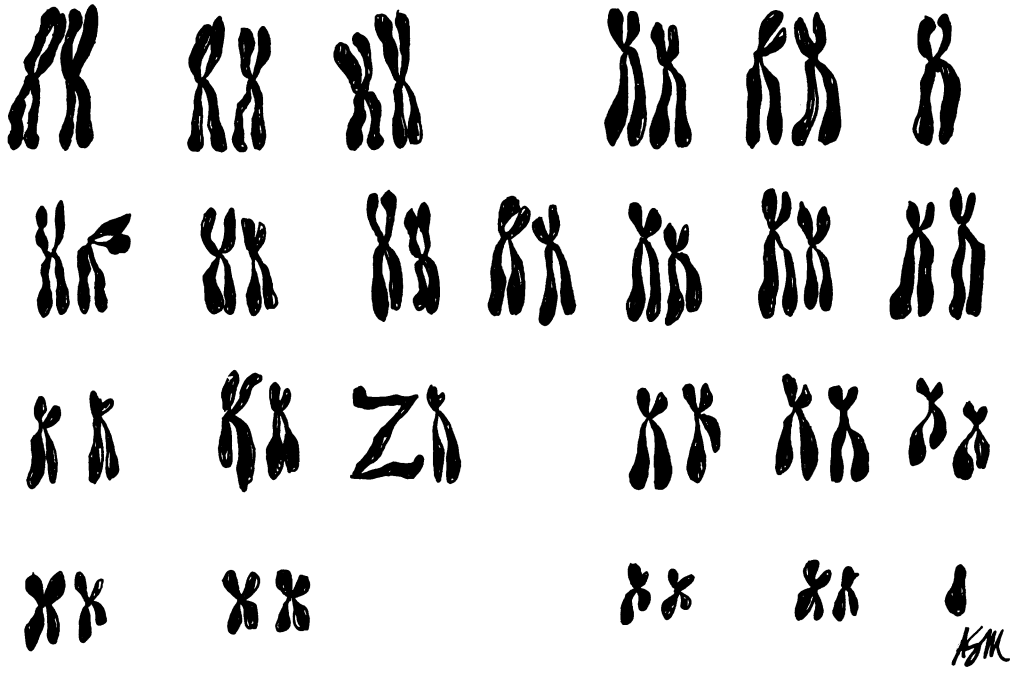

Teenage rebellion